

# TAXONOMY OF *BEBBIA* (COMPOSITAE: HELIANTHEAE)

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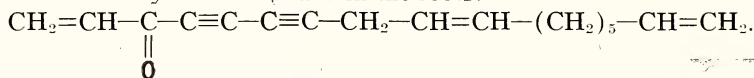
*Bebbia* is a genus of Mexico and the southwestern United States with its center of diversity in Baja California, where all 3 of its taxa occur. It is named for the botanist Michael S. Bebb, who worked on *Salix*. *Bebbia* is a small genus of little economic importance. Since it was proposed by Greene in 1885, it has been largely ignored, except for some controversy regarding its tribal position. A taxonomic treatment is provided here with keys and distribution maps.

## GENERIC RELATIONS

The generic position of what has come to be known as *Bebbia* has been questionable since it was first described as *Carphephorus* sect. *Kuhnoides* (Eupatorieae) by Asa Gray (1873). Greene renamed the taxon as a distinct genus, *Bebbia*, in the Heliantheae. It has certain superficial characteristics of the Eupatorieae, particularly a long plumose pappus and striate involucrel bracts. However, these characters are also found, although less frequently, in the Heliantheae. Other characters of *Bebbia* clearly unite it with the Heliantheae: the persistent chaff subtending each floret, the Helianthoid achenes, the style branches, and the deep yellow corollas.

King and Robinson (1970) note that the Eupatorieae can be easily separated from the Helenieae-Heliantheae complex on the basis of micro-characters. They describe anther appendages of Helenieae-Heliantheae as keeled with the abaxial surface concave and with a thickened central region. They also state that members of this group often have glands (not visible with a dissecting microscope) on the abaxial surface of the anther appendages. They report clusters of such glands in *Bebbia juncea*. Although I do not know how these characters hold up throughout the Heliantheae, King and Robinson's description of the anther appendages in *Bebbia* is correct. I examined a number of specimens of each of the 3 taxa in *Bebbia* and usually found a cluster of glands (rarely 1 or 2) on the abaxial side along the thickened central region of the anther appendage. To the extent that these characters are valid in distinguishing the Eupatorieae from the Heliantheae, they support the placement of *Bebbia* in the Heliantheae.

Naturally occurring acetylenic compounds are of taxonomic significance within the Compositae (Bohlmann et al., 1973). Recent examination of *B. juncea* by Bohlmann (pers. comm.) has established the presence of one acetylenic compound in the roots:



This compound is the most common thus far detected in the Heliantheae, occurring in 11 species of *Helianthus*, 3 of *Tridax*, 4 of *Galinsoga* (Bohlmann et al., 1973), and in one species of *Schistocarpha* (Bohlmann et al., 1976). However, it was not found in any of the 35 species of Eupatorieae examined (Bohlmann et al., 1973). Thus, there is chemical as well as morphological support for the placement of *Bebbia* in the Heliantheae.

Various suggestions have been made as to the position of *Bebbia* within the Heliantheae. It has been considered to belong to the Verbeninae or Madiinae (Greene, 1885) or Galinsoginae (Hoffmann, 1894, who followed Bentham, 1873; Torres, 1968). Stuessy (1977) places it in his Neurolaeninae, which he considers related to the Galinsoginae, the former distinguished from the latter in having alternate leaves, phyllaries of unequal length (increasing inward), lanceolate paleae, and setose pappus. Phyllaries of unequal length, lanceolate paleae, and setose pappus (characteristic of *Bebbia*) are found in members of Stuessy's Galinsoginae as well as his Neurolaeninae. Furthermore, *Bebbia* does not have alternate leaves. (The presence of alternate leaves is not diagnostic for the Neurolaeninae anyway since of the 2 core genera, *Neurolaena* has alternate and *Schistocarpha* has opposite leaves.) Thus, I believe *Bebbia* fits well within the Galinsoginae even as constituted by Stuessy. *Bebbia* appears close to *Tridax* (Galinsoginae) and not particularly close to *Schistocarpha* or *Neurolaena*, which differ from *Bebbia* in floral characters, i.e., in their truncate style branches, non-plumose pappus, glabrous achenes without distinct faces, and more chartaceous involucre. *Bebbia* is also related to *Dyscritothamnus*, *Clappia*, *Pseudoclappia*, and *Varilla*, which are treated as a distinct subtribe of the Heliantheae, the Varillinae, by Turner and Powell (1977) but are included in the Neurolaeninae by Stuessy (1977). If these genera, along with *Schistocarpha* and *Neurolaena*, constitute a natural group within the Heliantheae as Stuessy suggests, then *Bebbia* would appear to be transitional between the 2 subtribes, and it might prove taxonomically more expedient to recognize but a single large subtribe, the Galinsoginae, to include both Stuessy's Neurolaeninae and Turner and Powell's Varillinae.

The genera to which *Bebbia* probably is most closely related are *Dyscritothamnus* (Neurolaeninae) and *Tridax* (Galinsoginae), both of which may have radiate or eradiate heads. *Bebbia* and *Dyscritothamnus* are similar in habit and in many aspects of floral morphology (Table 1). Turner and Powell (1977) consider *Dyscritothamnus*, *Varilla*, *Pseudoclappia*, and *Clappia* to form a tightly knit group, alike in their succulent habit, distribution, and ecology, and having similar overall leaf and floral morphology. However, *Dyscritothamnus* seems to be more similar to *Bebbia* than the other genera in having a more pronounced plumose pappus, slender and more recurved style branches not appendaged at the

TABLE 1. COMPARISON OF *Dyscritothamnus* AND *Tridax* WITH *Bebbia*.

<i>Bebbia</i>	<i>Dyscritothamnus</i>	<i>Tridax</i>
Perennial shrubs	Perennial shrubs	Annual or weak-stemmed, perennial herbs
Pappus setose, uniseriate, plumose with lateral processes 0.1–0.3 mm long	Pappus setose, uniseriate, plumose with lateral processes 0.6–1.0 mm long	Pappus uniseriate, usually plumose, scales or bristles
Inner phyllaries wholly chartaceous, straw-colored with orange striae	Inner phyllaries wholly chartaceous, stramineous with orange striae	Inner phyllaries partially herbaceous, light green, often with purple margins, or wholly purple
Chaff with orange striae	Chaff with orange striae	Chaff usually with yellow-green striae
Outer phyllaries herbaceous	Outer phyllaries subscariosus	Outer phyllaries herbaceous
Lobes of disk corolla pubescent, tube densely glandular	Lobes and tube of disk corolla glabrous	Lobes of disk corolla usually pubescent, tube pubescent or glabrous
Leaves opposite throughout or opposite below and alternate above	Leaves alternate	Leaves opposite, or rarely alternate above and opposite below

top, more distinctly 3-angled, obpyramidal achenes, and similar chaff and phyllaries (Table 1). *Bebbia* also appears to be close to *Tridax* (Galinsoginae) and to approach *Tridax* in many of the characters that distinguish it from *Dyscritothamnus* (Table 1). Also, *Tridax* often has glandular-tipped trichomes on the peduncles and outer phyllaries, as are found in *Bebbia atriplicifolia*. These are not present in *Dyscritothamnus* and related genera discussed above. The achenes and floral morphology are similar in *Bebbia* and *Tridax*, although there is considerable variability within *Tridax* itself. *Bebbia* can be readily distinguished from both *Tridax* and *Dyscritothamnus* by the several characters listed in Table 1.

A chromosome number of  $2n = 9$  II has been consistently reported for the 3 taxa in *Bebbia*: *B. atriplicifolia* (Turner et al., 1973), *B. juncea* var. *juncea* (Turner et al., 1973), and *B. juncea* var. *aspera* (Powell and Turner, 1963; Solbrig et al., 1972; Sonora, Guaymas, *M. Whalen* 195, TEX). Chromosome numbers also support an affinity of *Bebbia* with the Galinsoginae and Neurolaeninae, genera of which are primarily based on  $x = 8$  and 9 (Stuessy, 1977). Chromosome counts for *Dyscritothamnus* have not been reported. *Tridax* has base chromosome numbers of  $x = 9$  and 10 (Powell, 1965).

## TAXONOMIC TREATMENT

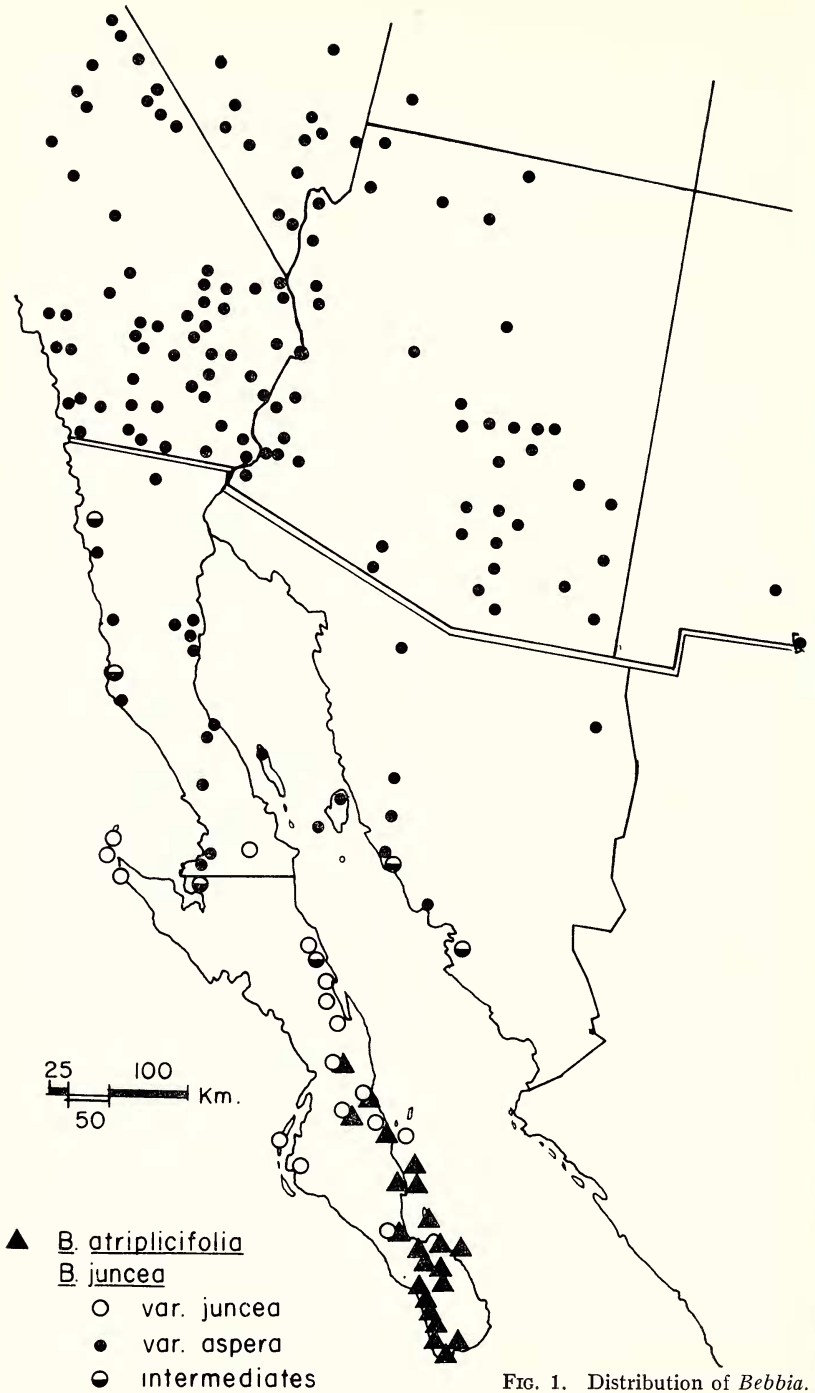
*Bebbia* was originally proposed by Greene (1885) to house 2 species: *B. atriplicifolia* and *B. juncea*, the latter containing 2 varieties. I. M. Johnston (1924) subsequently reduced *B. atriplicifolia* to a variety of *B. juncea*. For the reasons discussed below, I believe Greene's original treatment delimits better the natural taxa within *Bebbia*.

BEBBIA Greene, Bull. Calif. Acad. Sci. 4:179. 1885.—*Carphephorus*, sect. *Kuhnioides* Gray, Proc. Amer. Acad. Arts 8:632. 1873. LECTOTYPE (chosen here): *Bebbia juncea* (Benth.) Greene  $\equiv$  *Carphephorus junceus* Benth.

Perennial, strongly-scented, often leafless shrubs, low and spreading with upright annual branches or forming dense, rounded masses; the root thick, fusiform, woody, 1–5 cm in diameter (the basal portions with gray fissured bark); stems ribbed, glabrous or pubescent, leaves sparsely to moderately pubescent, sessile or petiolate, opposite throughout or opposite below and alternate above, blades linear to triangular and lobate, the margins entire to laciniately dentate; hairs of stems, leaves, and involucre simple, white, tuberculate-based, antrorsely-curved, 0.1–0.6 mm long (sometimes interspersed on the peduncle with glandular trichomes); heads discoid, 25–70 florets, campanulate, solitary or forming loose corymbose capitulescences; receptacle convex, chaffy; chaff 5.0–8.5 mm long, scarious, stramineous with red-orange striations and sometimes red-tipped, persistent, lanceolate, partly enclosing the achene; phyllaries 3–5 seriate, graduate, striate, unequal in length; outer series pubescent, herbaceous with chartaceous margins, inner series longer, becoming more glabrous and chartaceous; disk florets regular, the corolla 6.5–10.0 mm long, having a short glandular tube 1–2 mm long, a narrowly funnelform limb, and 5 broadly ovate, pubescent lobes; style branches ca 2 mm long, slender, exserted, recurved, with stigmatic lines on the inner surface running from base to tip; anthers linear-ob lanceolate, tapered to the base and with ovate-acute apical appendages ca 0.5 mm long; achenes 2.0–3.5 mm long, compressed, 3-angled, obliquely clavate with evident epigynous disk, black when mature, pubescent with ascending white hairs 0.2–0.6 mm long; pappus uniseriate, of 15–30 slender, white, subequal, plumose bristles as long as or longer than the corolla; base chromosome number,  $x = 9$ . (Figs. 1, 2).

Key to taxa of *Bebbia*

Leaves without distinct petioles, the blades narrow, linear to linear-ob lanceolate, entire or with one to a few lobes; peduncles and outer phyllaries without glandular hairs; perennial shrubs forming globose masses; heads solitary or few-clustered in loose corymbs borne on long branches. . . . . 1. *B. juncea*.



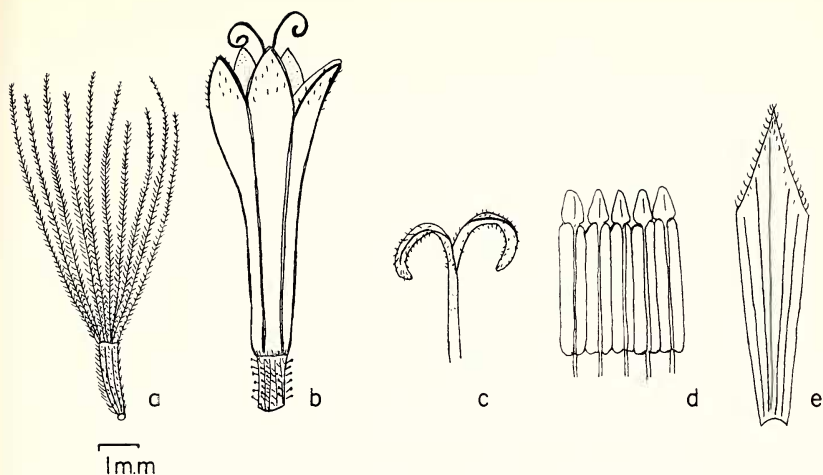


FIG. 2. Representative floral sketches of *Bebbia* (from *B. juncea* var. *aspera*, Clokey 8192, TEX). a, disc achene. b, disc corolla. c, style branches. d, stamens. e, chaff.

Involucral bracts imbricate and obtuse, rounded or mucronate, not acute; outer phyllaries ovate, 1–3 mm long, 1–4 mm wide, usually as wide as or wider than long; heads usually solitary, sometimes borne in a small corymb; central and northern Baja California. . . . . 1a. *B. juncea* var. *juncea*.

involucral bracts acute and not markedly imbricate; outer phyllaries narrow, lanceolate, longer than wide, 1–3 mm long, 0.7–1.5 mm wide; heads solitary or more often in open corymbs of a few heads; northern Baja California, Sinaloa, Sonora, and southwestern United States . . . . . 1b. *B. juncea* var. *aspera*.

Leaves with distinct petioles, blades hastate to laciniate-triangular with coarsely dentate margins; peduncles and outer phyllaries with glandular hairs; plants clambering, flat-topped, often scandent or semi-scandent on shrubs, trees, or rocks; capitulescence usually of many heads clustered in a compact corymb on short peduncles ca 1.5 cm in length; southern Baja California . . . . . 2. *B. atriplicifolia*

1. *BEBBIA JUNCEA* (Benth.) Greene, Bull. Calif. Acad. Sci. 4:180. 1885.—*Carphephorus junceus* Benth., Bot. Voy. Sulph. 21. 1884.—TYPE: Mexico, Baja California, Magdalena Bay, 1844, *Hinds s.n.* (Holotype: K, not seen; photograph of holotype, GH!).

*Bebbia filifolia* Jones, Contr. West. Bot. 18:80. 1933.—TYPE: Mexico, Baja California, Loreto, Cayuca Ranch, 23 Oct 1930, *Jones 27783* (Holotype: CAS!).



Perennial shrub with a dense crown of intricately branched, nearly leafless stems forming a rounded bush, 0.5–3.0 m high; upper stems lithe, woody, glabrous to hispidulous-pubescent, divergent at an angle of (10)30–45(55) degrees; leaves sessile, opposite below, alternate and often reduced to subulate bracts above, the blades narrow, linear to linear-oblongate, entire or with 1–5 deltoid to linear lobes, 0.5–6.0 cm long, 1–6 mm wide, moderately pubescent to canescent; peduncles 1.5–10.0 cm long, pubescent with simple, white trichomes; heads solitary or in small corymbs (2–5 heads) borne on the upper branches which are 5–8 cm long; outer phyllaries canescent; corollas yellow.

DISTRIBUTION (Fig. 1): Mostly in the Sonoran desert of northwestern Mexico and adjacent southwestern United States.

Blake (1945) took *B. filifolia* to be synonymous with *B. juncea*, i.e., he noted Jones' type specimen to be "*B. juncea* approaching var. *aspera*". The type of *B. filifolia*, however, appears to belong to *B. juncea* var. *juncea* since it has the more imbricate involucre and mucronate or rounded phyllaries characteristic of this taxon and was collected south of Comondu in the southern part of the range of var. *juncea*.

1a. *BEBBIA JUNCEA* (Benth.) Greene var. *JUNCEA*.

Bush 1–3 m high; stems smooth, glabrous to lightly pubescent; heads usually solitary, 1.0–1.7 cm long, 1.1–2.0 cm wide; phyllaries strongly imbricate in 3–5 series, obtuse, rounded or mucronate; outer bracts ovate, farinose, 1–3 mm long, 1–4 mm wide, usually as wide as or wider than long; inner bracts longer, narrower, 1–3 mm wide, 1.5–6.0 mm long, usually longer than wide (Figs. 3, 4a, 4b).

DISTRIBUTION (Fig. 1): Baja California from El Pilar (24°28'N) to Cedros Island (28°23'N), both on the peninsula and on islands offshore. Common on rocky or sandy soil between 5 and 1000 m, usually in washes and arroyos but also in the open desert. Flowering year round.

Plants of var. *juncea* collected south of Muleje, in the area of the type locality, have fewer (15–20) and broader phyllaries than those of plants to the north, which have 20–30 bracts per head. The leaves also tend to be larger in the southern forms. Heads of plants collected from basaltic cliffs of the Sierra Giganta above Pt. Escondido are particularly large, when pressed 2.5 cm wide and 1.3 cm long, with 50–60 florets per head.

1b. *BEBBIA JUNCEA* var. *ASPERSA* Greene, Proc. Calif. Acad. Sci. 4:180.

1885.—*Bebbia aspera* (Greene) A. Nels., Bot. Gaz. 37:273. 1904.—

TYPE: Greene cited "southeastern borders of California, and adjacent Arizona". Neotype (chosen here): United States, Arizona, Greenlee Co., mountains near Clifton, 3 Sep 1880, *E. L. Greene s.n.* (NY!).

Bush 0.5–1.5 m high; stems smooth and lightly pubescent or more pubescent and hispidulous; peduncles 1.5–6.0 cm long; heads 0.4–1.7 cm long, 0.4–2.0 cm wide, solitary or clustered in loose corymbs (2–5 heads) borne on long upper stems; involucre bracts in 2–4 series, weakly imbricate and acute; outer bracts narrow, lanceolate, canescent,



FIG. 3. Habit sketch of *Bebbia juncea* var. *juncea* (T. S. Brandegee s. n., UC).

1–3 mm long, 0.7–1.5 mm wide, usually longer than wide; inner bracts narrow, linear, longer, usually 3–7 mm long, 0.7–2.0 mm wide (Figs. 2, 4c).

**DISTRIBUTION** (Fig. 1): Northern Baja California, Sonora, and Sinaloa; southern California, Nevada, Arizona, southwestern Utah, New Mexico, and far western Texas where it is rare in the Franklin Mountains near El Paso. Common on rocky or sandy soil between 15 and 1450 m; in washes, canyons, and rocky stream beds in the desert, and on dry hillsides and gravel slopes. Flowering most of the year.



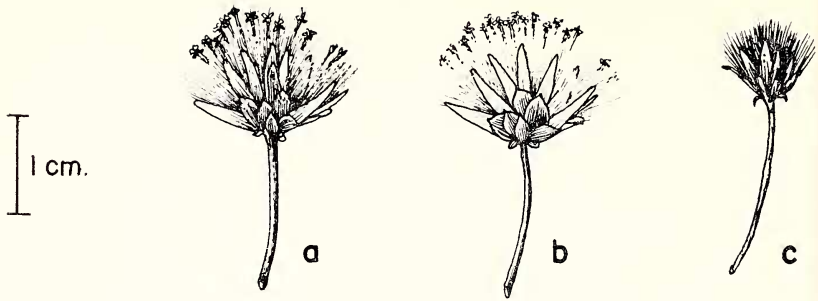


FIG. 4. Heads of *Bebbia juncea*. a, *B. juncea* var. *juncea* from the northern part of its range (*A. L. Haines s. n.*, UT). b, *B. juncea* var. *juncea* from south-central Baja (*Mason 1895*, US). c, *B. juncea* var. *aspera* (*Clokey 5948*, UT).

Nelson (1904) elevated *Bebbia juncea* var. *aspera* to specific rank for the following reasons: "I believe that no one who will take the trouble to compare the description of *B. juncea* from Cedros Island, which furnished the type, with the full description of the inland forms will question their distinctness." Geographical intergrades between vars. *juncea* and *aspera* link the two taxa. Therefore, I agree with Greene that this taxon should be treated as a variety and not as a distinct species. Morphological intermediates are designated on the distribution map (Fig. 1).

Involucration and shape of the involucral bracts, and *not* stem pubescence or size and number of heads, which Greene used to delimit the two varieties, are the most reliable characters in distinguishing these two taxa. Roughness of the stems is particularly variable. Plants of both varieties in Mexico have smooth, glabrous or almost glabrous stems, while in the United States plants may be smooth or rough-stemmed. There is a general trend for plants of var. *aspera* in the northern part of its range to be more hispid and to have smaller, more numerous heads, which are usually not solitary, but rather are borne in few-headed corymbs. Plants from Sonora and Sinaloa are closer to var. *aspera*, but occasionally approach var. *juncea*, especially in characters of the involucre.

2. *BEBBIA ATRIPLICIFOLIA* (Gray) Greene, Bull. Calif. Acad. Sci. 4:181. 1885.—*Carphephorus atriplicifolius* Gray, Proc. Amer. Acad. Arts 5:159. 1859.—*Bebbia juncea* var. *atriplicifolia* (Gray) I. M. Johnston, Proc. Calif. Acad. Sci., IV. 12:1197. 1924.—TYPE: Mexico, Baja Calif., Cape San Lucas, Aug 1859—Jan 1860, *L. J. Xanthus* 47 (Holotype: GH! Isotype: US!).

Plants with a stout woody base, forming dense, intricate, sprawling, flat-topped masses, 0.5–3.0 m wide, self-supporting or supported by other shrubs; stems brittle, pubescent, upper stems divergent at an angle of 40–85 degrees; leaves opposite, with distinct petioles, 3–17 mm long, blades hastate to triangular, 2.5 cm long, white tomentose, with coarsely dentate margins; capitulescence projecting above the plant, corymbose



FIG. 5. Habit sketch of *Bebbia atriplicifolia* (Carter 2261, UC).

with a clearcut branching system of usually 5–25 heads clustered on short peduncles; peduncles 0.3–4.0 cm long, on the average 1.5 cm in length, with stalked, glandular hairs and simple trichomes; heads 0.9–2.0 cm long, 1.0–2.5 cm wide with involucre bracts broadly acute, in 2–4 series, not markedly imbricate; the outer rows herbaceous, 1.3–5.0(–7.0) mm long, moderately pubescent with both simple and glandular hairs; inner rows more chartaceous and glabrous with the innermost bracts 4–9 mm long; involucre bracts and chaff often red-tipped; corolla yellow-orange to orange-red (Fig. 5).

DISTRIBUTION (Fig. 1): Common in gravelly or sandy soils between 5 and 1450 m from the southern tip of Baja California at Cape San Lucas north to Comondu ( $26^{\circ}03'N$ ); in washes and on dunes and granitic bluffs near the ocean, also frequent in arroyos and on rocky hillsides. Flowering year round.

Plants of this species are larger-headed to the north. At the southern margins of its range the heads of *B. atriplicifolia* have from 25–30 florets with average head size 1.3 cm long by 1.2 cm wide. At the northern extreme of its distribution, large-headed forms occur with from 35–60 florets per head and a usual head size of 2.5 cm long and 1.2 cm wide.

I. M. Johnston reduced *B. atriplicifolia* to varietal rank because "Although the two forms [*B. atriplicifolia* and *B. juncea*] seemed distinct in the field, a study of the material in the Brandege Herbarium has seemed to substantiate Mr. Brandege's statements (Proc. Calif. Acad. Sci. II, 2:180. 1889, and Zoë 1:271. 1890) that the forms approach each other too closely" (Johnston, 1924). These plants would appear more distinct in the field because they differ in habit. Furthermore, based on my study of herbarium material, including that from the Brandege Herbarium, the two taxa appear to be good species readily distinguishable by their habit, characters of the leaves and inflorescence, and the presence or absence of glandular hairs on the peduncles. The range of *B. atriplicifolia* overlaps in central Baja California with that of the more northerly *B. juncea* var. *juncea*, and the two have been collected in close proximity at four different localities. No sign of morphological intergradation can be inferred from herbarium material from these sites.

Brandegee (1889) reports finding connecting forms between *B. juncea* and *B. atriplicifolia* at Comondu and San Gregorio in Baja California. He distinguishes between the two taxa solely on the basis of ovate versus acuminate involucre bracts and lanceolate versus triangular leaves. The shape of the bracts will not differentiate between *B. juncea* as a whole and *B. atriplicifolia*. However, the characters listed in the present key easily separate the two taxa.

#### ACKNOWLEDGMENTS

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#### NOTES AND NEWS

THE "GERMINATION FLAP" IN CERTAIN GRAMINEAE.—In a recent paper (Madroño 23: 68-72. 1975), T. L. Rost & A. D. Simper report on "the germination lid" and its occurrence on lemmas of grasses. The statement is made that this structure was first observed in *Setaria* in 1949 by Keys (*Trans. Kansas Acad. Sci.* 52:474-477). This is quite incorrect. Hitchcock & Chase as long ago as 1910 recognized this feature and commented on it in their monograph of *Panicum* (*Contr. U.S. Nat. Herb.* 15: XIV + 396 pp). On page 18 they state, "fertile lemma chartaceous-indurated, typically obtuse, the nerves obsolete, the margins inrolled over an inclosed palea of the same texture, a *lunate line of thinner texture at the back just above the base, the radicle protruding through this at germination;*" (italics mine). That this "germination lid" was recognized as being characteristic of *all* genera of Paniceae by Hitchcock & Chase is indicated by the statement under the Tribe Paniceae, on page 26 of Hitchcock's Manual (U.S. Dept. of Agric. Misc. Publ. 200. 1935): "fertile lemma and palea indurate or at least firmer than the glumes and sterile lemma, a lunate line of thinner texture at the back just above the base, the rootlet protruding through this at germination."

Rost & Simper mention also that there is some question regarding the systematic position of *Antheophora* and *Olyra*. Although this might have been true several years ago, it is certainly not so today. Fifteen years ago, I published a detailed study of *Antheophora* (Reeder, J. R. in *Trans. Amer. Microscop. Soc.* 79:211-218. 1960) which left little doubt that this genus is a member of the Tribe Paniceae,